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2 Section II/4

3 **Animals and Humans in the Paleolithic**

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7

8 **The Deep Past is a Foreign Animal Country**

9 The Paleolithic is the oldest and longest period in human cultural history, traditionally defined
10 as a specific package of ecological, material, and behavioral conditions. It is thought to begin
11 with the appearance of the first human-made stone tools more than 3 million years ago and to
12 harbor the diverse human forager lifeways (mobile and semi-sedentary hunter-gatherers and
13 hunter-gatherer-fishers) developing in the context of the often-volatile climate shifts of the
14 Pleistocene (ca. 2.6 ma to 11.7 ka). The period formally ends with the onset of the Holocene,
15 the relatively stable warm phase of the last 12,000 years often uncritically associated with the
16 efflorescence of human cultures and the rise of so-called ‘civilizations’. The Paleolithic
17 frames a wide range of ecologies without any historical parallels; its animal and plant
18 assemblages therefore differ greatly from their Holocene counterparts, with now extinct
19 megafauna such as mammoths, giant sloths, and ‘terror birds’ frequently taken to signpost
20 these non-analogue worlds of the deep past. The Paleolithic is thereby commonly contrasted
21 with the later Neolithic period and its emergent agricultural, pastoral, and horticultural forms
22 of human life, even though the involved complexities defy such simple polarities. Human
23 history before the Holocene (henceforth: the deep past) nonetheless acts as a foil to more
24 recent time periods, as it is only in the latter that humans emerged as the dominant Earth-
25 system agents and re-structured the composition of the biosphere, drastically reducing the
26 biomass of wild animals in favor of humans and domesticated animals. Interrogating human-
27 animal relationships of the deep past is therefore arduous and riddled with often
28 underestimated epistemological challenges: we cannot simply adopt a presentist lens to
29 understand the unfamiliar worlds of the deep past and the unique, multifaceted forms of
30 human-animal interaction supported and perpetuated by them.

31 Since the deep past is studied in the present, it is always contested and perhaps
32 especially so in the age of ecological anxiety and looming catastrophe. We commonly exhibit
33 great confidence in the objectivity of the Paleolithic as a period, and how we analyze,
34 interpret, and narrate it, a sense increasingly compounded by the burgeoning natural and life-
35 scientific leanings of deep-time archaeologists, but this past remains ‘a foreign country’
36 inescapably dependent on present and imagined future conditions (Lowenthal, 1985). This is
37 why it is so important to reflexively engage with the problem of how the present shapes our
38 engagement with and understanding of the deep past, in particular with regards to human-
39 animal relationships, which have recently attracted critical attention across the humanities and
40 social sciences. They are too often stereotyped in service of a present compelled to progress
41 and overriding narratives of nature subjugation and control. Deep past human-animal
42 relationships present a burning lens of such Whig histories and are easily ‘othered’ – as a
43 prelude, alternative, or antithesis of what historicists call ‘modernity’. Although there is a
44 growing consensus among archaeologists that human-animal interactions constitute a key
45 dynamic in earliest human history and have shaped the human condition, they are still
46 frequently marginalized as an extension of natural history or a reflection of basic ecosystem
47 processes such as predator-prey relationships. Their scientific representations are therefore
48 strongly interlaced with the negotiation of supposed key thresholds in early human evolution
49 and broader imaginaries of life before ‘civilization’ or the ‘age of humans’.

50 Deep-time human-animal engagement is often treated as a monolithic category, as a
51 particular type of interaction tied to a specific mode of human life – nature-reliant, transient
52 foragers who do not produce foodstuff. Both humans and animals are commonly stereotyped
53 when their Paleolithic intersection is discussed. The animals are readily shoehorned as ‘wild’
54 with largely fixed species-level behaviors, while their human interlocutors are colored in
55 tropes of primitivism and Eurocentrism and are pictured as living in ‘wilderness’, either as
56 ‘noble savages’ and ‘conservation-minded Indians [sic!]’ (Anderson, 2005: 6) or as fierce and
57 suppressive predators (Shipman, 2017). This has made it difficult to pinpoint and discuss
58 meaningful relationships that are catered by both human *and* animal lives, and to recognize
59 their mutual constitution. Animals are relegated to the natural background of human history or
60 are examined exclusively in terms of their services for human foragers, as economic or
61 cognitive resources – ‘good to eat’, ‘use’ and/or ‘think with’. Belaboring this lingering
62 anthropocentrism is a core concern of the emerging project of multispecies archaeology,
63 which has highlighted the importance of changing forms of human-animal cohabitation and
64 co-sociality – past animals are also ‘good to live with’ (Hamilakis and Overton, 2013; Hill,

65 2021; Pilaar Birch, 2017). The tendency to shoehorn human-animal interactions of the deep
66 past continues to be an obstacle for such work, as it imprudently casts them as narrow or
67 limited in scope and diversity (Hussain, in press; Motta and Porr, 2023), and so essentializes
68 these relationships and deprives them of their plasticity and historicity.

69 The deep past is a foreign animal country not just because it is so difficult to
70 confidently walk it from a presentist human-centered standpoint or because the animals by far
71 outnumbered their Paleolithic human interlocutors (Hussain, 2023a), but also because of the
72 irreducible human biocultural diversity it hosts. The latter has two dimensions: 1) the richness
73 and diversity of past forager economies and cultures is still widely underestimated (Finlayson
74 and Warren, 2017), especially since ethnographically documented hunter-gatherer lifeways
75 likely represent a mere sub-sample of the total variability of such life; 2) the deep past was
76 populated by different human forms including our own species, Neanderthals, Denisovans,
77 and other early hominins with different behavioral and cultural repertoires respectively. This
78 pronounced human diversity adds much variability to Paleolithic human-animal interactions
79 and underscores the importance to not simply brush aside the human context. But it also
80 further complicates the study of such interactions as assumptions on the different human
81 forms weigh heavily on how we conceive of their entanglement with other animals. This is
82 chiefly reflected in influential archaeological debates on the relationship between
83 Neanderthals and our own species, reigniting the age-old ‘Ancients vs. Modern’ discourse
84 symptomatic for our difficulties of coming to grips with the foreign country that is the deep
85 past. Until recently, Neanderthals were customarily portrayed as incapable of sustaining
86 meaningful ties with other animals outside of predator-prey relations and beyond exploiting
87 their resources (Hussain et al., 2022; Wragg Sykes, 2020). The foreign country compels us to
88 remain vigilant and to cultivate a critical-reflexive attitude towards nonhuman animals and
89 their diverse and possibly non-analogue interactions with humans.

90

91 **Challenges and Sources of a Deep Prehistory of Human-Animal Relations**

92 Archaeological approaches to human-animal relations of the deep past continue to struggle
93 with their tacit commitment to Cartesian nature-culture binaries, separating humans from
94 other animals and the rest of nature, and so impeding the recognition of the full spectrum of
95 animal contributions. Such stipulations are certainly ironic given that nonhuman animals in
96 the present are increasingly recognized as cultural beings (Whiten, 2021). The equally
97 pronounced tendency to reduce human-animal histories to natural history, especially when

98 concerned with earlier human forms and time periods such as the Lower and Middle
99 Paleolithic, is merely the flipside of this preoccupation (Corbey, 2005). The second major
100 challenge is to belabor premises of human exceptionality and to move beyond
101 anthropocentrism (Boyd, 2017). An important task for human-animal archaeologies is
102 therefore not just to examine the role of animals in past human lifeways but also to critically
103 address, and if necessary defuse, one-sided narratives of control and domination. This
104 involves overcoming the dichotomization of ‘wild’ vs. ‘domesticated’ animals, detracting
105 from past relational pluralities and leading to somewhat misleading discussions as to the
106 social and societal role of animals under these two behavioral regimes (Armstrong Oma,
107 2010; Ingold, 1994; Knight, 2012). A key problem of interrogating the deep past is to unpack
108 and deconstruct ‘wildness’ and to search for more productive ways of describing shifting
109 power-relations and levels of control, tension, and care (Anderson et al., 2017), and to
110 recognize that autonomy and dependency (or heteronomy) are varyingly negotiated through
111 time and space and in relation to changing human and animal contexts (Hussain, in press).
112 Paleolithic studies can make an important contribution here as scholars are almost exclusively
113 concerned with wild animals and how these figure in and interfere with human projects. The
114 synchronic and diachronic investigation of the intersection between early foragers and wild
115 nonhuman animals can thus help in developing a basic understanding of the intricacies and
116 complexities of ‘naturecultures’ and how animals and humans have always co-shaped each
117 other, although in different ways and with different consequences.

118 The third challenge is also an opportunity and leads us to the sources of human-animal
119 archaeologies of the deep past. Scholars must rely exclusively on material remains that have
120 survived the millennia and can inform on past human-animal interaction. To this end,
121 zooarchaeologists traditionally study animal bones to show which animals shared the
122 environment with humans, what these environments looked like, and how humans used
123 animal resources, including which animals they hunted and gathered, how they processed
124 them, and how these engagements changed through time and space. Complementary to the
125 analysis of animal fossil remains, archaeologists also examine what can be termed animal-
126 related material culture – human-made objects that either depict animals or use their body
127 parts as raw materials, for example for subsistence tools. Bioarchaeologists have recently
128 developed a suite of methods to extract more derived, molecular data from fossilized animal
129 materials. Stable isotope analyses provide information on the climatic and environmental
130 context of past animal life as well as on the dietary preferences and mobility patterns of
131 different animals, and so can be compared to similar human-related data. New protein-based

132 methods (proteomics) together with the study of ancient DNA (aDNA) help to characterize
133 population structures and demographic histories, which in turn can be linked to
134 reconstructions of past human behavior. This reliance on material remains is sometimes cast
135 as a severe epistemic disadvantage as such evidence does not directly ‘speak to us’ and so
136 makes it more difficult to trace meaning and cultural significance in the deep past, yet it can
137 be argued that this renders such evidence simultaneously less burdened by human filters and
138 thus promotes the direct study of past animal life and its human entanglements. This is
139 illustrated by the archaeological recovery of trace fossils (ichnology), which can help to
140 qualify human-animal cohabitation, for example by indicating the use of similar tracks by
141 humans and megafauna around 20,000 years ago in New Mexico (Bennett et al., 2021), or
142 probe into animal physical impacts on the landscape, for instance sloth/armadillo tunnel-
143 building (Hussain, 2023a) Archaeology can so deploy a unique ‘animal lens’ (Specht, 2016)
144 and to pioneer a deeply interdisciplinary approach to the study of historically changing
145 human-animal assemblages and multispecies systems, which is now also increasingly
146 acknowledged by animal history scholars (Bonnell and Kheraj, 2022). Yet in comparison to
147 historical and more recent archaeological archives, deep-time records tend to be coarse-
148 grained, and their chrono-spatial resolution is often limited, which, compounded by
149 taphonomic distortions, shifts the attention to broad-scale patterns and long-term perspectives,
150 while enforcing a healthy source-critical optic. Deep-time archaeological evidence lends itself
151 to big-picture investigations of human-animal relations and is therefore key in writing new
152 more-than-human histories and sociologies of an aged planet.

153 This entry deliberately shifts the attention away from the classic meat-eating and
154 hunting narrative and the modernist image of increasingly intense animal exploitation in the
155 course of the Paleolithic period, eventually leading to the management and control of
156 nonhuman animals (Starkovich, 2018). It instead foregrounds alternative windows into deep
157 past human-animal relationships, organized in relation to key sources and themes – some of
158 them long-standing, others emerging – and resisting a march of progress. This treatment
159 remains necessarily selective and to some extent reflects my own preoccupation(s), but I hope
160 it nonetheless provides a useful overview and sense of a discipline which is about to
161 considerably expand its original zooarchaeological reach and strives towards a more holistic
162 reconstruction of multifarious, tangled human-animal life in the deep past.

163

164 **Visual Culture as Direct Evidence of Significant Animal Others**

165 Animal visual culture comprises the diverse forms of animal imagery produced by Paleolithic
166 foragers around the world, and as such provides a multifaceted but compelling perspective on
167 human-animal relations in this period. Generally speaking, animal imagery is never an
168 unfiltered reflection of the natural environment, but demonstrates selectivity and meaning,
169 foregrounding particular animals and animal collectives, and not others. As such, animal
170 visual cultures administer direct evidence of the sweeping significance of the respectively
171 rendered animals. The fact alone that animals, and not humans, clearly dominate the
172 representational content of Paleolithic visual culture supports this recognition. At least some
173 animal-oriented imaging practices were further aimed to evoke the respective animals, to
174 render them *co-present* with humans, and so to enable communication and social interaction.
175 In addition, there is growing appreciation that differences in imaging practices through time
176 and space have probably less to do with human cognitive capacities, but are more likely
177 rooted in different ways of living with, seeing, and intersecting with animal others (Hussain
178 and Floss, 2015a; cf. Bird-David, 2006 for an anthropological perspective).

179

180 *Mobile art*

181 Mobile art refers to visual culture small enough to be carried along with other forager
182 equipment across the landscape. There are two types of animal mobile art: 1) objects shaped
183 as animals such as two or three-dimensional sculptures, and 2) objects that bear animal
184 depictions, for example painted, picked, or engraved. Both types constitute figurative art and
185 there is no apparent chronological hierarchy between them. Hussain and Floss (2015b) have
186 argued that large keystone megafauna was often at the center of mobile art-making during the
187 earlier part of the Upper Paleolithic and that this changed after the Late Glacial Maximum
188 (LGM) with increasing emphasis placed on medium-sized ungulates. They have explored how
189 the cultural salience of mammoth and cave lion in the mobile art of the Aurignacian in
190 southwestern Germany (ca. 40-30 ka) is anchored in the keystone agency of these two
191 powerful animals (ecosystem engineering, apex predation). A lion-like being is also depicted
192 on the famous, ca. 30,000 years old stone plaque from the Middle Stone Age (MSA) of Apollo
193 11 in South Africa (Rifkin et al., 2015). Porr (2004, 2015) has discussed how the mobile art of
194 the Swabian Aurignacian negotiates the human-animal boundary, reflected especially in the
195 well-known lion-human hybrid, and how animals mediated the construction and negotiation
196 of gender ideals. It has also been suggested that this mobile art embodies deep-seated cultural
197 memory, and thus the central place of the respective animals in human imagination, social

198 identity and world-making (Porr, 2010). Hussain (2019) has argued that the distinct set of
199 burnt owl-shaped clay figurines and ivory ornaments from the Moravian mid-Upper
200 Paleolithic (ca. 31-27 ka) reflect the unique exposition of foragers and philopatric owls, and
201 so the latter's key role in the construction of a sense of place. The assemblage of small clay
202 figurines features also lion, bear, wolverine, rhino, mammoth, and cervids. Many of these
203 figurines seem to have been intentionally buried relatively shortly after their production,
204 highlighting their role in conjuring up animal others and relating to them.

205 In the Late Upper Paleolithic, especially the Magdalenian (ca. 20-15 ka), the focus
206 increasingly shifts towards deer and other ungulates, notably reindeer and horse (Maier,
207 2015). This re-organization of mobile image worlds is accompanied by an encroachment of
208 functional everyday artefacts with animal imagery. Spear thrower handles, projectile points
209 and so-called *bâton percé* are increasingly ornamented with animal engravings. At the
210 Magdalenian sites of Gönnersdorf and Andernach in the German Rhineland, shist plates are
211 engraved with horse and mammoth images but also seals and a raven (Dutkiewicz, 2021).
212 These images are probably entangled with multiple aggregating forager groups and their
213 storytelling and cultural exchange, with mammoths and seals likely representing exotic
214 animals. Magdalenian mobile art also increasingly references aquatic ecologies and their
215 inhabitants. Brown and colleagues (2017) have argued that recurrent associations of eel, fish
216 and horse imagery, often foregrounding horse heads, in the French Magdalenian and
217 subsequent Azilian may point to the importance of fishing affordances in beaver-shaped
218 landscapes, notably the use of severed horse heads to capture eel, an ethnographically well-
219 documented strategy. There is also a notable uptake of non-stationary bird engravings and
220 carvings towards the second half of the Upper Paleolithic, especially water-related species. At
221 Mal'ta (ca. 23-15 ka) in the Russian northeast near Lake Baikal, an exceptional assemblage of
222 ivory-carved bird figurines probably representing swans, cranes and geese/ducks were found
223 alongside mammoth, fish and snake images (Lbova and Volkov, 2016). In northern Europe,
224 Final Paleolithic mobile art, often engraved bones or stone plates, features especially horse
225 and aurochs depictions (Naudinot et al., 2017), while horse and elk are well-represented
226 among three-dimensionally rendered figurines (Veil et al., 2012).

227

228 *Parietal art*

229 Parietal art is defined as the stationary imagery mounted on, and often embedded in, mineral
230 landscapes features such as rockshelters, caves, or other open-air rock formations, collectively

231 also labelled rock art. In Europe, animal-themed parietal art is primarily a phenomenon of
232 Upper Paleolithic *Homo sapiens* populations, although Neanderthals have recently been
233 shown to be likely responsible for some painted lines and dots in Spain and so-called ‘finger
234 flutings’ in the cave of La Roche-Cotard (Marquet et al., 2023). Together with abstract signs
235 and geometric forms, animal imagery dominates the art. Overall, horse and bison motifs are
236 numerically most important, followed by deer, ibex, mammoth and aurochs (Sauvet, 2019),
237 even though there are important regional and temporal differences. In Western Europe,
238 parietal art is often divided into two larger art-making cycles: a pre-LGM phase comprising
239 the early and mid-Upper Paleolithic and a post-LGM Magdalenian climax. In the period
240 between ca. 34 and 21 ka (first cycle), Djindjian (2013) distinguishes three broader areas of
241 ‘iconocenose’: a continental zone east of the Rhône characterized by co-association of
242 mammoth, rhinoceros, feline and bear images – Jean Clottes’ ‘not hunted and dangerous
243 animals’; an Atlantic zone with a preference for horse, bison/aurochs and mammoth, and
244 Mediterranean zone characterized by horse-aurochs linkages. Some of the earliest figurative
245 animal engravings, probably from former rockshelter walls, have been discovered in early
246 Aurignacian sites in the French Vézère valley (ca. 40-30 ka), including images of horse, ibex,
247 felines, bovids and rhino (Bourrillon and White, 2015). A unique assemblage of mainly
248 engraved horse, aurochs, deer/doe and ibex dates to the Solutrean and Badegoulian shortly
249 before and during the LGM, the later part of which is well-represented in the the open-air
250 landscapes of Côa valley and Siege Verda in Portugal. In the second, Magdalenian parietal
251 art-making cycle is more diversified and mostly dominated by horse and bison depictions,
252 with reindeer images playing an important role in some areas.

253 At Tuc d’Audoubert in the French Pyrenean foothills, late Magdalenian foragers have
254 modeled two large bison figures from cave clay and bison images are found in key locations
255 of the cave interior, with floating bison motifs, sometimes up-side down, placed in key
256 passageways (Bégouën et al., 2009). The position, arrangement and design of the images
257 reflect the key role of the animals in human underground experience, cultural practices, and
258 ways of seeing the world. Les Trois-Frères in the same larger cave system, yielded a rare
259 example of a scenic owl representation. While these images, and bird depictions in general,
260 are notably rare in European Upper Paleolithic parietal art, it is interesting that strigiform
261 depictions first appear in selected liminal cave art contexts of the Middle Magdalenian, before
262 snowy owls are systematically targeted for their bones, feather and claws in the Upper
263 Magdalenian (Hussain, 2021). Reindeer imagery is especially important in southwestern
264 France (Davidson, 1999), where reindeer not only played an anchoring role in the sustenance

265 of the respective Magdalenian societies but may have been non-migratory (Fontana, 2017).
266 Interestingly, the total frequency of reindeer depictions in Western European parietal art is
267 comparable to anthropomorphic renderings, and the relative subordination of reindeer in
268 Magdalenian parietal art further contrasts with mobile art patterns, suggesting divergent roles
269 of different material practices in negotiating human-animal relationships. Brumm et al. (2021)
270 have argued that the recurrence of warty pig images in the early parietal art of Sulawesi,
271 featuring unique morphological traits, points to complex human-pig relationships, and
272 possibly mutuality (Brumm, 2023), from as early as 45 ka onwards. Although the reality of
273 Pleistocene rock art in the Americas remains contentious, the presence of pictorial
274 representations of megafauna such as giant sloths, extinct elephants, other trunked ungulates
275 and large camelids highlights the temporal overlap between humans and megafauna (Iriarte et
276 al., 2022) and the significance of the latter in early human lifeworlds. Some of these animal
277 renderings may also reflect mnemonic practices and human attempts to conjure up significant
278 others as these slowly disappeared from the landscape at the end of the Pleistocene.

279 The structure and logic of parietal animal image-making, especially well-documented
280 in Western Europe, generally suggests that larger mammals proffered a fundamental lens to
281 encounter, engage with and imagine the world. As ‘installation art’ (Sakamoto, 2019), animal
282 imagery is frequently co-structured and even motivated or pre-empted by rock shapes and
283 configurations inherent in physical cave environments, in turn suggesting that the imagery
284 materializes visual affordances and perceptive preoccupations of Upper Paleolithic people.
285 This is also reflected in the partiality of many animal depictions, which often consist merely
286 of indicative lines or incomplete shapes to be appended by the human perceiver. Living with
287 animals has therefore critically shaped Paleolithic ways of seeing and understanding the world
288 and to signify meaning in it. Hussain (2023b) has argued that animal agency has also more
289 directly contributed and shaped parietal-art making, for example cave bear markings that were
290 imitated by past people and frame and/or integrate human-made images, as in Aldène cave
291 close to the French Mediterranean coast where Upper Paleolithic people added a backline
292 engraving to a set of prominent cave bear claw marks to ‘complete’ a mammoth. Parietal art
293 can so critically inform the study of past human-animal-landscape interactions and helps to
294 understand how hunter-gatherer cultures of the deep past negotiated and fabricated meaning,
295 perceived their world, and were shaped by nonhuman animals in the process.

296

297 **Zoo-Materiality and Human Selectivity: Differential Use and Transformation of Animal**
298 **Raw Materials**

299 Zoo-materialities, material culture made of animal body parts and products, allow the
300 examination of the organizational consequences of human-animal relations in terms of human
301 collective action, techno-economic logics and cosmovisions. As habituated patterns of past
302 human behavior, they permit to carefully approach questions of perception, selection and
303 signification grounded in lived realities and interactions, and as such how forms of animal
304 agency crystallize in the archaeological record in shifting circumstances. Zoomateriality so
305 sheds light on ‘anthrozotechnical’ relations (Doré and Michalon, 2017) and illustrates how
306 animals precipitate their archaeological materialization, thus framing a potent microcosm of
307 past human-animal interaction and meaning-making. From a broader anthropological
308 perspective, they often reflect fluid boundaries between human and nonhuman bodies,
309 qualities (traits, capacities), and worlds, how animals are woven into the fabric of human
310 culture and everyday practice as *pars pro toto*, and/or circulate and partake as ‘gifts’ in
311 interspecies exchange relations (Hill, 2019; Hussain, in press; Nadasdy, 2007), predicated or
312 not on notions of the ‘giving environment’ (Bird-David, 1990).

313

314 *Organic technology*

315 Bone, antler, horn and ivory technology not merely informs on the instrumental repertoire of
316 deep-time forager tool-use, it provides evidence for how animal materials participate in the
317 construction and reproduction of human-animal relations. Middle Paleolithic Neanderthals in
318 Europe (ca. 125-50 ka) are a good example of such meaningful, differential material
319 engagements. As prime predators, Neanderthals had access to a wide range of large mammals
320 and birds, but they were highly selective in co-opting particular materials and animal body
321 parts for material transformation and tool-use (Wragg Sykes, 2020). Some Neanderthals
322 targeted paws and especially feet bones of bears to be used as retouchers for stone working,
323 others opened skulls of younger elephants to extract the brain and used their ribs for the
324 manufacture of pointed sticks or lances, many fur/skin smoothers were made of aurochs and
325 bison ribs, and the femura of deer served as organic retouchers (Hussain et al., 2022). Horse
326 incisors were sometimes also employed to modify and rework stone tools. Neanderthal bone
327 use is generally more common and varied than often argued. At Chez-Pinaud in France where
328 reindeer remains otherwise dominate the assemblage, bones from larger ungulates are almost
329 twice as often used by Quina Neanderthals for tool-making, and especially for multi-tools (M

330 Baumann et al., 2023). Quina Neanderthals are often described as specialized reindeer hunters
331 with a unique lifestyle in relatively cold open steppe environments, yet reindeer bones seem to
332 have not been preferentially modified, often used as fuel, and if transformed turned into
333 special end-smoothed and beveled tools (Baumann et al., 2022). At the early Middle
334 Paleolithic site of Schöningen in Germany, horse metapodials were deployed as ready-made
335 tools for bone marrow extraction, direct percussion and as anvils. The site has also yielded a
336 large humerus of a saber-tooth cat, probably already rare in this period, co-opted as a
337 retoucher (Serangeli et al., 2015). The manipulation of a giant deer phalanx in the terminal
338 Middle Paleolithic of Einhornhöhle in Germany (Leder et al., 2021) equally showcases the
339 relevance of material engagement with an animal of reduced dietary significance. Other early
340 Neanderthals and/or *Homo erecti* in Central Europe but especially in Italy and Israel produced
341 distinct elephant bone artefacts including imitations of stone handaxes, iconic Lower
342 Paleolithic tool forms, which Barkai (2019, 2021) has interpreted as evidence for the domain-
343 transgressing significance of proboscideans for early human life in this timeframe. In contrast
344 to saber-tooth cats and giant deer, these animals dominated and shaped these human
345 landscapes and were also hunted and scavenged, thus pervading human lifeworlds and being
346 deeply entangled with human practice and thought.

347 European Upper Paleolithic foragers (ca. 50-15 ka) have similarly produced a variety
348 of organic technologies and began to systematically target antler and horn of specific cervids
349 and transformed mammoth ivory into a range of functionally differentiated tools including
350 projectile points and rope-making devices, especially before the LGM. In Southwestern
351 Germany, tool-making during the earlier Upper Paleolithic was closely intertwined with
352 mammoth ivory (chisels, retouchers, projectiles, flutes), while in the subsequent mid-Upper
353 Paleolithic no such ivory tools were manufactured anymore and animal bone became the
354 focus of organic tool-use again, especially mammoth ribs (Münzel et al., 2017). In the post-
355 LGM late Upper Paleolithic of coastal Iberia, whale bones emerged as an important raw
356 material for pointed tools, circulated within hunter-gatherer social networks (Lefebvre et al.,
357 2021), and sometimes transported many hundred kilometers inland (Langley and Street,
358 2013), underscoring the their cultural significance. A much older single tooth of a sperm
359 whale most likely employed as a hand-held pressure flaker has been found at Contrebandiers
360 cave at the Atlantic coast of Marocco (ca. 120-90 ka), associated with spatula-like bone tools
361 used for carnivore fur extraction and processing and selectively made from shaft bones of
362 gazelle and aurochs (Hallett et al., 2021). At the end of the North African Later Stone Age (ca.
363 15 ka), bone points recovered from the Moroccan site of Tatoralt also testify to animal

364 selectivity: the two major species – gazelle and hartebeest (antelope) – from which the points
365 were manufactured together represent only ca. 13% of the total of the site’s large mammal
366 fauna (Desmond et al., 2018), demonstrating clear subsistence-decoupled animal preferences
367 and patterns of material engagement. Final Paleolithic foragers (ca. 15-12 ka) preferentially
368 co-opted reindeer and elk bones and antlers for their material culture, manufacturing t-shaped
369 axes and smoothed-beveled objects (Płonka et al., 2011; Wild et al., 2022), some of them
370 ornamented with abstract patterns and geometric motifs, foreshadowing early Holocene
371 hunter-gatherer zoomaterialities and preoccupations.

372

373 *Personal ornaments*

374 The term personal ornaments describes small, nonstationary items worn on the human body.
375 As ‘body adornments’, these objects extend and reinforce the body as the ‘first ornament’
376 (Menninghaus, 2011) and ‘enculture it’ (Nowell and Cook, 2021). Depending on their modes
377 of suspension and attachment, they broadcast *embodied* human-animal relations, and often
378 break down bodily and essential species-difference. Neanderthals have used the talons of
379 large powerful diurnal eagles as ornaments and probably extracted feathers, especially of
380 darker colors, of larger raptors for the same. Hussain and colleagues (2022) have argued that
381 this interest was likely rooted in lived interspecies intimacies resulting from regular human-
382 raptor co-associations at carrion sites. Some late Neanderthals in Spain also perforated, and
383 sometimes painted, large bivalve shells (Nowell, 2023). In Africa and the Levant, early *Homo*
384 *sapiens* groups began to systematically collect sea snails of the Nassariidae family, especially
385 *Nassarius*, for personal ornamentation between ca. 150 and 80 ka (Sehassseh et al., 2021).
386 These were typically minimally modified, and sometimes took advantage of natural
387 perforations, circulated within extended social networks, and were included in human burials,
388 generally pointing to the cultural significance of coastal and estuary ecologies and their
389 nonhuman inhabitants for some MSA populations. In the European early Upper Paleolithic,
390 shells and mollusks continue to be important as body ornaments but considerably diversify
391 (Vanhaeren and d’Errico, 2006). The Aurignacian culture alone has provided evidence for
392 more than 150 different types of personal ornaments, including animal teeth. Early and mid-
393 Upper Paleolithic societies in Western and Central Europe often preferentially used mammoth
394 ivory for bead production (Wolf and Heckel, 2018), exemplified by the famous Sunghir
395 burials which included >40 ivory arm bands and >13000 ivory beads as well as ivory rings,
396 disks and bipointed spears (Trinkaus and Buzhilova, 2018). Sunghir is also notable for its

397 selective inclusion of perforated fox teeth. In Southwestern Germany, the transition from the
398 earlier to the mid-Upper Paleolithic marks a shift in animal-oriented ornamentation practices,
399 from an initial emphasis on ivory to a focus on animal teeth (Münzel et al., 2017). Fox teeth
400 pendants are especially frequent in the Aurignacian, less so in the Gravettian, and virtually
401 disappear in the Magdalenian. The large-scale aggregations sites mid-Upper Paleolithic
402 aggregation sites in Moravia have also yielded large numbers of fox teeth ornaments,
403 alongside perforated wolf teeth.

404 Based on a detailed assessment of Aurignacian systems of personal ornamentation in
405 southwestern France, White (2007) has shown that selectivity of animal teeth modification is
406 strongly decoupled from patterns of unmodified teeth in the same faunal assemblages.
407 Carnivore teeth generally play an important role as body ornaments in the Aurignacian.
408 Chronological and inter-site variability is pronounced in this period, but broader patterns are
409 discernible. At Brassempouy, red deer and wolf/fox teeth ornaments dominate the earlier
410 Aurignacian layers, while wolf/fox and bear monopolizing the later layers and modified red
411 deer teeth disappear almost altogether (White, 2007). Similar compositional differences can
412 be observed at Isturitz: the Protoaurignacian assemblage is dominated by ornamental bovid
413 teeth alongside notable numbers of modified fox and red deer as well as some hyena teeth,
414 while the younger Aurignacian assemblage is more balanced and also includes modified
415 horse, wolf and lion teeth but lacks hyena and red deer teeth ornaments (White, 2007). An
416 interest in the fluidity of materials, bodies and capacities is further demonstrated by several
417 facsimiles (exact copies of animal teeth in other materials) in French Aurignacian ornamental
418 assemblages, for example cervid teeth imitated in ivory and stone at Brassempouy or
419 impersonated marine shells made of ivory at La Souquette (White, 1992). These examples
420 illustrate that the referenced animals themselves but also the raw materials used greatly
421 mattered to early Upper Paleolithic people and were carefully selected.

422 In the Solutrean of Cantabrian Spain, animal teeth and shells are equally important for
423 ornamentation: the former are dominated by hoofed animal, especially red deer
424 complemented by ibex and horse, the latter by gastropods and dentalia (Álvarez Fernández,
425 2013). The regional ornamental assemblages also include perforated bird bones, fish
426 vertebrates and suspended shark teeth. In France, dentalium is the preferred ornamental shell
427 during the Solutrean (Taborin, 2004). This preference is dissolved in favor of a wider diversity
428 of seashells with a strong emphasis on tower shells (Turritellae) during the following
429 Salpétrian (ca. 24-22 ka) of the Rhône area (Boccaccio, 2021). New research seems to show

430 that the Solutrean-Badegoulian transition in France, accompanied by a radical re-organization
431 of stone artefact and organic technologies, retains relatively varied ornamental shell
432 assemblages, even though shell procurement and circulation patterns are notably re-
433 configured (Peschaux, 2021). In the subsequent Magdalenian of Central Europe, fossil rather
434 than lived mollusks were collected, while in the Cantabrian Magdalenian marine and
435 lacustrine species were targeted for personal ornamentation. In parallel, cervid teeth become
436 more prevalent, especially sawn-off reindeer incisors and atrophied canines of red deer,
437 sometimes accompanied by marmot and ibex teeth (Álvarez-Fernández, 2009). Around 70 red
438 deer canines were found at the exceptional Late Upper Paleolithic burial site of Saint-
439 Germain-La-Rivière in southwestern France, preferentially obtained from young stags, and
440 circulated and exchanged within long-distance forager networks (Vanhaeren and d’Errico,
441 2005). Fox teeth are also common in some north-west European Magdalenian ornamental
442 assemblages, but at Gönnersdorf in Germany for example mostly premolars of the animals
443 were harnessed, whereas earlier Upper Paleolithic societies in southwestern Germany
444 suspended almost exclusively fox canines (Baumann et al., 2020).

445 Different animals were conjured in other parts of the world, referencing varying
446 animal environments and symbolic ecologies. Pansani and colleagues (2023) have recently
447 reported a small collection of human-modified osteoderm bones of giant sloths from the LGM
448 layers of Santa Elina cave in central Brazil, some of which are perforated. These objects likely
449 illustrate the lived significance of this keystone megafauna with pronounced terraforming
450 capacities in the context of the earliest occupation of South America, pre-empting the later co-
451 optation of their borrowed structures for rock art (Hussain, 2023b). The continued use of
452 ostrich eggshell for bead-making across large parts of Africa, Asia and Australia throughout
453 the later part of the Pleistocene points to the equally elevated status of this flightless bird in
454 early human forager lifeways (e.g., Miller and Wang, 2022). Again, human-ostrich relations
455 have likely even deeper roots as showcased by the unique tradition of decorated ostrich
456 eggshell containers from the South African MSA (Texier et al., 2013).

457

458 *Burials and structured depositions*

459 As burials and other structured depositions indicate highly curated behaviors, inter alia in the
460 context of what has been termed *mortuary theatre*, they are privileged archaeological contexts
461 to map significant human-animal relationships (Hill, 2000). In the Levant, the Neanderthal
462 child burials of Qafzeh 11 and Amud 7 are associated with red deer antlers and a red deer

463 mandible respectively, thereby contrasting with the likely *Homo sapiens* male adult burial of
464 Skhul V, which included a boar mandible. The association between red deer and pre-adults
465 has been linked to red color symbolism also reflected in preferences of ochre use, possibly
466 framing a broader context of meaning-making for red deer significance. In the European
467 earlier Upper Paleolithic, the burial evidence is scarce and the structured deposition of animal
468 body parts alongside human bodies was apparently not practiced to negotiate and reproduce
469 human-animal relationships. The mid-Upper Upper Paleolithic, by contrast, yielded rich
470 evidence for human-animal burial associations (Pettitt, 2011). Notable is especially the
471 neonate double burial from Krems-Wachtberg in Lower Austria (ca. 26 ka), whose bodies
472 were overlain with a mammoth scapula supported by a tusk, covered with >30 ivory beads,
473 and embedded in a thick layer of red ochre (Einwögerer et al., 2006)

474 The Magdalenian multi-burial of Neuwied-Irlich in the German Rhineland was found
475 in conjunction with a perforated and decorated cervid tooth pendant and an antler point
476 (Orschiedt, 2018). The slightly later terminal Late Paleolithic child burial of La Madeleine in
477 France comprised >1200 perforated shells, two perforated deer canines and two fox teeth. Its
478 exceptional status resonates with the previously mentioned burial of Germain-La-Rivière. The
479 Late Paleolithic burial of Los Azules in northwest Spain was associated with the skull of a
480 badger, the fragment of a deer antler and unperforated shells, whereas the complex human
481 burial or deposition site of Aven des Iboussières in the French Rhône valley with the remains
482 of >400 human individuals of likely terminal Paleolithic age (ca. 12-10 ka) features >1000
483 perforated shells, naturally perforated pike vertebrae, perforated and ornamented animal long
484 bones and some other mostly fragmentary decorated animal bones, teeth and mandibles of
485 pig, aurochs, beaver, rabbit and hedgehog alongside at least 200 incised and perforated red
486 deer canines (Grünberg, 2013). The Italian burial record from the Epigravettian period (ca.
487 15-12 ka) is also exceptionally rich and includes a whole range of contexts with mixed human
488 and animal remains, mostly shells and red deer teeth but also molars from horse and aurochs
489 as well as the jawbone of a roebuck (Orschiedt, 2018).

490 At Bonn Oberkassel, one of the few final Magdalenian burial sites in Central Germany
491 (ca. 13-14 ka), a male-female double burial stained in red ochre was found in conjunction
492 with a partial skeleton of a morphological dog, a bone pin and a carved cervid. A recent re-
493 analysis of the dog remains has shown that two animals were buried, one of which was only 7
494 months old as it died and was perniciously ill from distemper (Janssens et al., 2018), pointing
495 to the affective context of the animals' deposition. Other Late Paleolithic examples of human-

496 dog co-burials are Ein Mallaha (ca. 15-11 ka) and Hayonim Terrace in Israel (ca. 11-10 ka)
497 (Morey and Jeger, 2022). The earliest dog burials without humans date to around 10 ka and
498 come from Koster and Stillweg II at the lower Illinois river in the eastern United States (Perri
499 et al., 2019). Fox remains were similarly intertwined with deceased human bodies, for
500 example in the later Epipaleolithic and especially the Natufian of Israel and the wider Levant
501 (Maher et al., 2011), a practice continuing into the subsequent Neolithic of the region.

502 The careful burial of a gracile female at Hilzon Tachtit from the final Natufian (ca. 12
503 ka) in Israel further showcases the careful deposition of animal body-parts pregnant with
504 meaning, including the segment of an aurochs' tail, the skull of a marten, the articulated
505 forearm of a wild boar, the shell case of a tortoise and the upper wing tip of a golden eagle
506 (Grosman et al., 2008). Caching of animal ornaments together with human remains is possibly
507 in evidence for the French Badegoulian rockshelter site of Lachaud, indicating their role as
508 cultural capital or *valuta* in some Upper Paleolithic forager contexts. At the Late Upper
509 Paleolithic mammoth graveyard of Volchia Griva in Western Siberia, a portion of an Arctic
510 fox hemimandible, the tooth of a fox, and a large rib fragment of a mammal were enclosed in
511 the cavity of a distal mammoth femur and deposited at the site (Leshchinskiy et al., 2023),
512 pointing not only to the significance of this 'beastly' place but also evoking comparisons with
513 wrapped collections of meaningful items (bundles) in Indigenous cultures.

514

515 *Infrastructure*

516 Hunter-gatherer infrastructure is another key context of brokering human-animal relations.
517 The significance of past animals may also be reflected in the way they and their body parts are
518 entangled with and implicated in human-built features or structures. Infrastructure can on the
519 one hand facilitate and alter interspecies encounters, for example at monumental shell midden
520 sites in the MSA of South Africa or Incipient Jomon of Japan. The Late Paleolithic shell
521 midden of Ban Non Wat in Thailand has even yielded a complete Eld's deer deposition
522 alongside human burials (Higham and Thosarat, 2019). On the other hand, it can promote
523 place-making and living in and with structures made of animal bodies can help to foster
524 understandings as animals as an integral part of human society. An example for this are the
525 exceptional mammoth bone structures of the middle and late Upper Paleolithic of the Central
526 and East European plains (Iakovleva et al., 2012; Soffer, 1989). Otte (2014) has specifically
527 argued the unique mammoth materiality of the Mezinian reflects such deep-running co-
528 sociality between the Desna river and the Urals after the LGM. In contrast, the famous

529 circular mammoth bone structure of Kostenki 11 (25-24 ka) has been shown to have merely
530 housed ephemeral, relatively short-term human occupations, pointing to its ceremonial and
531 monumental role rather than a function as dwelling (Pryor et al., 2020). Sablin and colleagues
532 (2023) have recently reinforced this argument at the Late Paleolithic site of Yudinovo, where a
533 number of circular mammoth bone structures are now interpreted as monumental middens
534 erected in the context of communal gatherings and ritual activities in the course of which the
535 structures were buried again. Mammoths so feature in the construction of cultural landscapes
536 and become inscribed into their materiality. At the early Epipaleolithic aggregation site of
537 Karaneh IV in Jordan, place-making is also mediated by animals. A human tibia was found in
538 a pit with gazelle horn cores and mandibles, and a buried human body, probably associated
539 with one of the dwelling structures, had a pair of gazelle horns near the head (Maher et al.,
540 2021). In the Late Upper Paleolithic cave art site of La Garma in northern Spain, a single cave
541 lion individual was brought deep into the cave to remove the fur with still attached claws next
542 to human-assembled stone structures (Cueto et al., 2016). These examples show that human-
543 landscape relations were shaped by animal-implicating practices and but that different animals
544 were entangled with different human projects in different times.

545

546 **Animal Agency, Food-Web Dynamics, and Human-Animal Co-Evolution**

547 Archaeological evidence also bears directly on animal behavior of the deep past and broader
548 ecosystem dynamics involving both humans and other animals. Newer bioarchaeological
549 insights thereby powerfully undercut the wild-domestic polarity traditionally deployed to
550 make sense of Paleolithic human-animal relations. They demonstrate that Paleolithic animals
551 exhibit considerably behavioral plasticity making it difficult to model their agency as a mere
552 response to climates and natural environments and point to co-evolutionary constellations
553 within which nonhuman animals exerted significant *initiative*. The complexities of climate-
554 mediated behavioral flexibility in nonhuman animals has been outlined for ibex in northern
555 Spain across the Solutrean-Magdalenian transition (Jones et al., 2020), while general niche
556 redundancy and elevated levels of niche partitioning seem to have characterized the wider
557 Eurasian mammoth steppes ecosystem (Schwartz-Narbonne et al., 2019), further supported by
558 microwear animal teeth data reflecting pronounced dietary plasticity of late Pleistocene
559 ungulates (e.g., Rivals and Álvarez-Lao, 2018; Rivals and Semprebon, 2011). Broadly
560 climate-decoupled dietary diversity on the sub-species level may have been a key factor in the
561 adaptation of Pleistocene bears (Münzel et al., 2014) and notably wolves, whose dietary

562 strategies exhibit complex lead-and-lag patterns in relation to documented morphological
563 changes, for example in the cranio-dental make-up (Flower et al., 2021). As already
564 mentioned above, reindeer developed at least two ecotypes – highly migratory and quasi-
565 sedentary – for example in the Late Upper Paleolithic of southwestern France and during the
566 Middle Paleolithic of the Rhône valley (Britton et al., 2023; Fontana, 2017). These insights
567 underscore the noteworthy *historicity* of animal behavior and suggest that flexible animal
568 responses to broader changes in climates, ecosystems and perhaps human ecologies constitute
569 an important context for shifting human-animal relationships.

570 Animal populations were similarly impacted by human behavior, for example when
571 humans encroached the carnivore guild and re-configured carnivore assemblages (Faurby et
572 al., 2020) or when later Pleistocene human dispersal and ecosystem agency mediated global
573 megafaunal extinctions, even though the extent of human involvement continues to be
574 discussed and likely differed across continents and regions (Barnosky et al., 2004). Some
575 human populations also exerted considerable foraging pressure on animal others, well-
576 documented for example for shellfish across the MSA-LSA (Later Stone Age) transition in
577 South Africa (Klein and Steele, 2013). Body size data of mountain gazelle at the passage from
578 the Pleistocene to the Holocene in the southern Levant also suggest that intensifying human
579 exploitation re-configured the animals' availability on the landscape (Munro et al., 2022).
580 This example shows how human-induced changes in animal behavior, ecology and biology
581 can spur distinct responses in human behavior and culture, especially when humans become
582 increasingly dependent on the candidate species, and so may usher in coupled co-evolutionary
583 trajectories. The dynamics within past human-animal assemblages therefore greatly depend on
584 the precise historical context of both human and animal behavior and their specific
585 intersection, informing emerging human-animal relationships.

586

587 *'Feral' ecologies and incipient synanthropes*

588 Hussain (in press) has recently argued that even in interactive contexts with non-domesticated
589 animals, it is often misleading to conceptualize animal behavior as autonomous, unassisted or
590 self-reliant – as fully separable from its human ecology. Supposedly 'wild' animals often
591 orient their behavior towards their human landscape co-inhabitants, and so respond and adapt
592 to early human behavior. While deep-time archaeologists have traditionally focused on the
593 resource affordances provided by nonhuman animals, we can similarly ask what resource and
594 living affordances past foragers have offered to other animals. An important window into

595 development of such early human-oriented behaviors is the study of palaeo-synanthropy
596 (Baumann, 2023). Palaeo-synanthropes are animals who benefit from and thrive in human
597 neighborhoods and human-shaped environments, often by taking advantage of the
598 anthropogenic food-getting opportunities. Baumann and colleagues (2020) have shown that
599 some Upper Paleolithic red foxes have accessed a new synanthropic feeding niche in the
600 Aurignacian of southwestern Germany (ca. 40-30 ka), sustained this niche throughout the
601 subsequent Gravettian, but changed their dietary behavior again the Magdalenian. The
602 behavior of foxes is thereby interlinked with human behaviors, as the Aurignacian and
603 Gravettian of the region are characterized by intense hunter-gatherer presence and rich
604 archaeological deposits, while human settlement becomes more ephemeral during the
605 Magdalenian and domestic dogs coevally enter the arena. A similar connection has been
606 proposed for mid-Upper Paleolithic foragers and common ravens in Moravia. These earlier
607 Gravettian ravens are argued to have taken advantage of human-accumulated carcasses of
608 larger herbivores and especially mammoths close to human habitation sites and in turn
609 became important for human quotidian experiences and lifeways, as reflected in the use of
610 their feathers (Baumann, Hussain et al., 2023; Hussain, in press). Human settlement in this
611 spatiotemporal context is unusually intense and shows pronounced occupational fidelity,
612 features forager infrastructure including possible storage and waste disposal areas, and
613 exhibits evidence for the exclusion of larger carnivores. Significant shifts in trophic level
614 between regions or periods, for example as observed for Arctic foxes across the Gravettian-
615 Epigravettian transition in Lower Austria (Reiss et al., n.d.), may equally point to human-
616 assisted re-configurations of animal dietary ecologies.

617 Given the key role of hunter-gatherers as ecosystem ‘knitters’ (Crabtree et al., 2019), it
618 is therefore important to consider the often subtle but consequential involvement of
619 Paleolithic foragers in the assembly and evolution of food-webs and animal ecosystems.
620 These impacts can be significant factors modulating lived human-animal relationships, alter
621 the exposition and relevance of other animals, and so precipitate material engagement and
622 meaning-making. Importantly, the ‘feral’ ecologies that come into view in this way – animal
623 behaviors influenced by human projects but eclipsing human control – defuse simplistic views
624 of human priority in tailoring or even dictating situated human-animal interaction. Animals
625 like foxes and ravens can be said to showcase considerable *initiative* and to steer humans
626 towards particular behavioral and cultural trajectories. Such co-evolutionary dynamics with
627 distributed and messy power-relations may also underlie some early image-making practices
628 and so shape human material and cultural practices (Brumm, 2023). Another model case is

629 presented by the origin of the house mouse thought to have emerged in the context of
630 ecological niche incursion of settled Natufian forager societies in the Eastern Mediterranean
631 Levant around 15,000 years ago, who engaged in extensive wild plant gathering and
632 processing (Snir et al., 2015), providing competitive advantages to commensal mice living
633 close to human settlements (Weissbrod et al., 2017).

634

635 *Canine companions*

636 Paleolithic human-wolf relationships need to be understood as negotiations of latent conflict,
637 tension, facilitation, and care. As apex predators of their ecosystems, wolves and hunter-
638 gatherers were preeminent resource competitors but they also promoted each other as
639 paramount carcass accumulators, and, although difficult to corroborate archaeologically,
640 potentially engaged in varied forms of interspecies cooperation (Pierotti and Fogg, 2017). As
641 illustrated by ethnohistoric evidence and Indigenous oral history, this may have involved
642 collaborative foraging (Barsh and Marlor, 2003) and landscape learning, as wolves are often
643 said to have shown people how to hunt and make a living in novel and largely unknown
644 environments (Fogg et al., 2015). The relationship between Paleolithic foragers and wolves
645 intensified after the LGM, as wolves attained a central position in food-webs and broader
646 ecosystems as other large predators gradually dissipated. Non-coincidentally, genetic evidence
647 tracing the origin of domestic dogs back in time suggests that the roots of wolf domestication
648 lie somewhere between 30 and 10 ka. Wolf domestication has been highlighted as a watershed
649 event in human evolution with major implications for human hunting prowess, economic
650 intensification, and sociality. Paleolithic dogs are not only cast as the first companion species
651 to form permanent bonds with humans and so become an integral part of human forager
652 groups, they may have also crucially assisted in human dispersals, for example as a means of
653 transportation, as *Homo sapiens* set out to become a global species. Shipman (2017) has
654 argued that dogs rendered humans an irresistible ecological force and so catalyzed late
655 Pleistocene megafaunal extinctions when our species began to spread into all continents. But
656 there is currently little evidence for the presence of companion dogs accompanying early
657 human dispersals into Europe, Asia, Oceania, or the Americas, and based on the available
658 evidence it seems more likely that humans and dogs began to form more stable bonds when
659 the former consolidated their settlement in different regions of the world.

660 In Europe, the earliest accepted dog remains come from the Late Upper and Final
661 Paleolithic (ca. 17-12 ka), with important early records in the Italian Epigravettian and the

662 Spanish Magdalenian (Boschin et al., 2020; Hervella et al., 2022). Combining genetic,
663 morphological and ecological information, Baumann and colleagues (2021) have drawn
664 attention to the high morphological and genetic diversity of early domestic dogs at the
665 Magdalenian site of Gnrshöhle in the German Hegau (ca. 16-15 ka), pointing to the recurrent
666 taming and cross-breeding of wolves and dogs and the existence of diverse wolf ectomorphs.
667 This may indicate an extended process of tripartite human-wolf-dog interaction and the larger
668 synanthropic background of early dogs in Upper Paleolithic forager societies, which is
669 consistent with dogs being generally rare in Upper Paleolithic burials. Wherever they were
670 included in human burials, such as at the above-discussed later Magdalenian site of Bonn-
671 Oberkassel, the evidence currently postdates the earliest examples of wolf taming and
672 possible domestication for several millennia. Dog remains become nonetheless more frequent
673 as we approach the Pleistocene-Holocene boundary and are for example well-documented in
674 post-Magdalenian contexts (Azilian, Laborian) in Western Europe (Boudadi-Maligne et al.,
675 2016), where dogs are often seen as part of a larger package of adaptations involving
676 composite, bow-and-arrow-involving hunting technologies enabling broad-spectrum forager
677 economies in increasingly closed woodland environments, contrasting the (peri)glacial
678 steppe-tundra conditions of human-wolf interaction and co-living. The increasing
679 entanglement of humans and dogs, then, may have ultimately foreshadowed the eventual
680 departure from Ice Age forager lifeways and nature relations.

681

682 **Conclusion: The Paleolithic as ‘Humanimal’**

683 The study of human-animal relationships in the deep past is an exciting enterprise and sheds
684 light on how being human always involved to *be with animals* and to arrange oneself with
685 their worlds, behaviors, and projects. The Paleolithic period is therefore an important puzzle
686 piece in the larger quest to understand what it means to be human, as being human, to speak
687 with Anna Tsing (2012), ‘*is an interspecies relationship*’ (emphasis added). A dedicated
688 animal lens, without necessarily breaking with the long-standing archaeological interest in the
689 diversity and evolution of past human behavior, helps to unpack the myriad ways in which
690 animals came to be entangled with human life and shaped human material, social, cognitive,
691 and cosmological realities. Our deep hunter-gatherer past – comprising >99% of all human
692 history – must therefore be understood as a co-production of humans and animals. With
693 Donna Haraway (2003), the Paleolithic so comes into view as *humanimal* – as the emergent
694 product of the creative coming together of humans and animals. The humanimal condition of

695 the Paleolithic thereby varies considerably from other periods, hosting unique dynamics and
696 relational logics, zoo-materializations, and cultural representations.

697 To unveil the humanimal Paleolithic requires not only to embrace a holistic,
698 multidisciplinary approach to varied forms of species co-living and its distinct archaeological
699 consequences but also a firm commitment to the possible otherness of the deep past. The
700 latter calls for critical conceptual engagement with assumptive architectures, stereotypes, and
701 Whig histories, often tainted in Eurocentric and racist tropes of interpretation, imagination,
702 and narration. As part of this larger call to decolonize the study of deep-time human-animal
703 relationships, it is also pertinent to overcome one-sided notions of nature ‘red in tooth and
704 claw’ and to find new creative ways to interrogate interspecies collaboration and mutuality,
705 precisely because such relationships are notoriously difficult to recognize in the
706 archaeological record. Equally important will be the confrontation of long-standing empirical
707 biases foregrounding certain animals – notably large terrestrial mammals – but not others, and
708 so impeding the crystallization of more inclusive human-animal histories.

709

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